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OHIO'S PROMISCUOUS SUNFLOWERS[1]

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The promiscuity of plant species leading to hybridization is not new to plant science. It has, however, been a controversial topic in plant systematics for a long time. For many it has been a fascinating topic, not merely because of the event of hybridization, but because of the possible evolutionary effects it may have on the process of speciation or the possible deterrent to speciation, or in fact, on the reversal of speciation.

Linneaus suggested the possible hybrid origins for several plant species. In the 1800's and early 1900's, many botanists refused to recognize hybrids, partly because they interfered with the neat and orderly filing of herbarium material. Even so, many authors reported and discussed hybrids and hybridization through the 19th and 20th centuries. Until the early 20th century, most reports of hybrids and hybridizations were based on general observations and, in most instances, not accompanied by scientific data or analysis. Instead, most of the literature deals with the descriptive approach and the mere reporting of putative hybrids in various plant groups. Only recently have scientists turned their attention away from the descriptive approach to the more fundamental question, which is what are the significant short-range and long-range evolutionary effects of hybridization?

Scientists have used the term hybridization in many different ways. To some the crossing of pure line individuals that differ by a single gene constitutes hybridization. Some genetists and plant breeders regard hybridization as the crossing between inbred lined, such as in the production of hybrid corn differing by many genes. Others regard hybridization as the crossing between different species, such as the horse and the donkey. There seems to have been inconsistency in the use of the term. The most acceptable definition has been proposed by Stebbins *et al* (1977) as the crossing between populations having different adaptive peaks or complexes. It makes no difference whether these populations are members of different genera, species, subspecies of the the same species, or races of the same species. It is significant that such populations have developed during their evolutionary history some degree of isolation and/or isolating mechanisms, weak or strong, that have led to some degree of genetic divergence.

Ploidy Levels

Three ploidy levels can be found among Ohio's native sunflowers (table 1). Ten species are diploids, 3 are tetraploids and 2 are hexaploids. One species, *H. decapetalus,* exists at the diploid level and the tetraploid level and often in the same population and without morphological markings. Further-

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[2]PRESIDENTIAL ADDRESS—Presented at the 90th Annual Meeting of the Ohio Academy of Science held at Wooster College, Wooster, Ohio on 25 April 1981. Dr. T. Richard Fisher, Professor of Botany at Bowling Green State University, served as President of the Academy during 1980-1981. He received the B.S. degree from Eastern Illinois State University in 1946 and the Ph.D. from Indiana University in 1950. He served on the faculty of Appalachian State University from 1954-56 and joined the faculty of the Botany Department at The Ohio State University in the fall of 1956. He was appointed Chairman of the Department of Biological Sciences at Bowling Green State University in 1968 and served in that capacity until 1974. A Fellow of the Academy since 1958, Dr. Fisher has chaired the Ohio Flora Committee and served on the Executive Committee on two previous occasions. He served as consultant to the Indian Government during the summer of 1966 as a member of the A.I.D. Program. He is the author of many scientific papers including Volume 4, *The Compositae of Ohio* (in preparation), and is a member of Sigma Xi and Beta Beta Beta.

more, it may intergrade with *H. microcephalus* at the diploid level and *H. hirsutus* and *H. strumosus* at the tetraploid level.

TABLE 1

Ploidy levels of Ohio sunflowers (Helianthus).

Diploids (n = 17)*	Tetraploids (n = 34)*	Hexaploids (n = 51)*
H. mollis Lam.	—	—
H. occidentalis Ridd.	—	—
H. divaricatus L.	—	—
H. decapetalus L.	*H. decapetalus* L.	—
—	*H. hirsutus* Raf.	—
—	*H. strumosus* L.	*H. strumosus* L.
H. giganteus L.	—	—
H. grosseserratus Mart.	—	—
H. maximiliani Schrad.	—	—
H. microcephalus T. & G.	—	—
H. angustifolius L.	—	—
H. annuus L.	—	—
—	—	*H. tuberosa* L.

*n = Chromosome number.

TABLE 2

Natural hybrids among Ohio sunflowers (Helianthus).

	Hybridize with	
H. mollis (n=17)*	x	*H. divaricatus* (n = 17)*
	x	*H. giganteus* (n = 17)
	x	*H. grosseserratus* (n = 17)
	x	*H. occidentalis* (n = 17)
H. divaricatus (n = 17)	x	*H. microcephalus* (n = 17)
	x	*H. giganteus* (n = 17)
	x	*H. occidentalis* (n = 17)
	x	*H. grosseserratus* (n = 17)
H. hirsutus (n = 17)	x	*H. strumosus* (n = 34, 51)
H. tuberous (n = 17)	x	*H. strumosus* (n = 51)
H. giganteus (n = 17)	x	*H. grosseserratus* (n = 17)
	x	*H. divaricatus* (n = 17)
	x	*H. maximiliani* (n = 17)
	x	*H. microcephalus* (n = 17)
	x	*H. occidentalis* (n = 17)
H. grosseserratus (n = 17)	x	*H. maximiliani* (n = 17)
	x	*H. occidentalis* (n = 17)
	x	*H. tuberosus* (n = 17)
H. maximiliani (n = 17)	x	*H. angustifolius* (n = 17)
H. decapetalous (n = 17, 34)	x	*H. hirsutus* (n = 34)
	x	*H. strumosus* (n = 34, 51)

*n = Chromosome number.

Helianthus decapetalus at the tetraploid level has apparently hybridized with *H. annuus* in the distant past and given rise to *H.* x *multiflorus,* which exists as a common garden ornamental (Heiser and Smith 1960).

Natural Hybridization

With so much learned about *Helianthus* by C. B. Heiser, Jr. and his students in the past thirty years, it may appear that hybridization is rampant and that species boundaries are blurred resulting in difficult if not impossible identifications. On the contrary, the Ohio species preserve their genotypes quite well. It is quite rare to find hybrids and even more rare to find a hybrid swarm. The naturally occurring hybrids involving Ohio's sunflowers are presented in table 2. Not all of the possible hybrid combinations have been detected in the state but based on the many publications of Heiser, and on my own observations, they can be expected. Certainly, hybridization occurs more frequently in this genus than most genera of flowering plants.

Named Hybrids of Ohio Sunflowers

Hybridization between species often results in frustration for those people who must deal with the preservation and the filing of specimens in herbaria and museums. The result is often species with taxonomically blurred boundaries causing precise determination virtually impossible.

The International Code of Botanical Nomenclature states that hybrids may be designated by two methods. First, hybrids can be given names, thus conforming to the binomial system. The second method is the designation of such specimens by formulae by merely citing the hybridizing species. In the first instance, the hybrid between *Helianthus grosseserratus* Mart. and *H. salicifolius* A. Dietr., although unknown as a hybrid at the time, was described as a species and named *H. kellermanii* Britt. Later when it was determined that it was actually a hybrid, it was named *H.* x *kellermanii* Britt. (Long 1955), the x designating the hybrid nature of the specimen. The International Code permits the treatment of hybrids in either manner and for this reason, there are binomial names that have been applied to naturally occurring hybrids. While I usually prefer to use formulae to designate hybrids, binomial names exist in the literature (table 3) and especially for Ohio sunflowers.

and Guard 1958). We should keep in mind that one of the strongest forces in bringing about evolutionary change is the hybridization of species with different adaptive peaks or complexes, particularly in disturbed environments where new habitats are likely to be available to hybrid progeny.

The discovery of hybridizing populations of species merely reveals the event with few evolutionary implications. The observation and study of hybrid populations over a long period of time should reveal something about the nature of the population with respect to evolutionary change. The present study involves a hybrid swarm of these two species of sunflowers in a disturbed habitat in south central Ohio in which hybridization has occurred repeatedly for more than twenty-two years, the length of the study period.

TABLE 3

Named hybrids of Helianthus that either occur or may occur in Ohio.

H. x *ambiguus* T. & G. (designated by Long, 1954) (*H. divaricatus* x *H. giganteus*)
H. x *brevifolius* E. E. Wats. (designated by Jackson & Guard, 1957). (*H. grosseserratus* x *H. mollis*)
H. x *cinereus* T. & G. (designated by Jackson & Guard, 1957). *H. mollis* x *H. occidentalis*)
H. x *divariserratus* Long. 1954. (*H. divaricatus* x *H. grosseserratus*)
H. x *doronicoides* LAM. (designated by Jackson, 1957). (*H. giganteus* x *H. mollis*)
H. x *glaucus* Small. (designated by Smith & Guard, 1958). (*H. divaricatus* x *H. microcephalus*)
H. x *intermedius* Long, 1954. (*H. grosseserratus* x *maximiliana*)
H. x *kellermanii* Britt. (designated by Long, 1954). (*H. grosseserratus* x *salicifolius*)
H. x *laetiflorus* Pers. (designated by Clevenger & Heiser, 1963). (*H. rigidus* x *H. tuberosus*)
H. x *luxurians* E. E. Wats. (designated by Long, 1954). (*H. giganteus* x *H. grosseserratus*)
H. x *multiflorus* L. (designated by Heiser, 1960). (*H. annuus* x *H. decapetalus*)

Natural hybridization in *Helianthus* has been demonstrated in the numerous publications by Heiser and his students and need not be further elaborated on here. The main thrust of this investigation is an attempt to determine the effects of hybridization between two species of sunflowers, *Helianthus microcephalus* T. & G. and *H. divaricatus* L., over a 22 year study period.

Helianthus divaricatus (fig. 1) is one of the most common perennial sunflowers. Its range includes Arkansas, Missouri and Oklahoma, as well as nearly all the states east of the Mississippi River. Even with a rather extensive record of hybridization, this species is remarkably constant, occurring in open, usually dry habitats along fence rows, roadways and occasionally along woodland borders.

Helianthus microcephalus(fig. 1) is also a common species with its center of distribution primarily in the southeastern states extending northward into central Ohio and Indiana, occurring primarily in woodland borders and open woods.

It is well documented that these two species of sunflowers hybridize locally and form hybrid swarms, usually in disturbed habitats where their ranges overlap (Smith and Guard 1958).

Location and History of the Population

The hybrid swarm, the subject of the present study, is located on a hillside with a southwest exposure a few miles southwest of Lancaster, Ohio along state route 33 and about 1.5 miles west of Sugar Grove in a disturbed upland habitat above Neotoma, an ecology study area of Ohio State University for many years. At the beginning of the study period in 1958 and for an undetermined number of years before, the disturbed habitat was maintained by the annual cutting of the vegetation by maintenance crews of the local telephone company to prevent over-growth of the lines. The width of the study area within the maintained area was approximately 75 yards wide and 1.5 miles long. In 1962, the telephone line was abandoned and the prevailing woody species of oak, maple and hickory were again permitted to dominate the area.

The exact date before 1958 when the initial hybridization and subsequent backcrossing occurred and the swarm was established is not known. Since 1958, the repeated crossing and backcrossing has probably resulted in the population containing progeny of every generation to at least F_{22}.

FIGURE 1. Drawing of *Helianthus divaricatus* L. (left) and *H. microcephalus* T. & G. (right). Drawn at about ¼ natural size.

METHODS

The data for study were obtained from population samples of at least 24 plants taken every other year during the study period beginning in 1958 and ending in 1980. The population samples were analyzed by the Hybrid Number Method (Gay 1955, 1960), which is a modification of the Hybrid Index Method described by Anderson (1949) and used since that time by many workers to detect hybridization in populations. The Hybrid Number Method is a modification in that it is used in combination with the Hybrid Index Method. Its chief advantage is that it permits more meaningful averages of hybridizing populations. Furthermore, it enables the complex data of populations to be summarized by two statistics that are not limited by considerations of normality, unimodality or by accepted usage. It enables large numbers of population samples that contain hybrids to be compared by graphing the mean hybrid number against the mean hybrid index as employed by Gay (1955) and Fisher (1966). The Hybrid Number Method deals with three components of the population: the parental species, the F_1 hybrids, and the many segregates and backcross hybrids.

The hybrid index was prepared by scoring the following characters: leaf base angle (an indication of leaf shape), petiole length, head diameter, leaf surface and branching. These characters were selected because they easily separate these species.

Plants of each sample were first numbered and scored for each character. The raw scores were then grouped and assigned values from 0-4. Therefore, the total hybrid index for a plant representative of *H. divaricatus* would be 0, while a plant representative of *H. microcephalus* would be 20.

After the hybrid index for each plant in the population was determined, its hybrid number was computed in the following manner. Since the hybrid index scale extends from 0-x, the hybrid number scale extents from 0-x/2. From the hybrid index 0 to x/2, the hybrid number equals x minus the hybrid index. From these data, the mean hybrid index and the mean hybrid number of the population was computed.

A population consisting of "pure" *H. divaricatus*, sampled and analyzed according to the Hybrid Number Method, would graph at the 0 end of the scale, while a "pure" sample of *H. microcephalus* would graph at the 20 end of the scale (fig. 2). On the other hand, a population consisting of an equal proportion of the two parental species and F_1 hybrids would graph exactly in the center of the triangle. The reason for this precise location is that ⅓ of the population consisting of "pure" *H. divaricatus* would score a value of 0 for hybrid index and 0 for hybrid number. The ⅓ of the population consisting of *H. microcephalus* would score 20 on the hybrid index scale and 0 on the hybrid number scale.

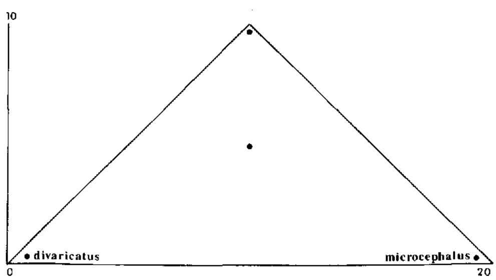

FIGURE 2. Four hypothetical populations of *Helianthus* analyzed by the Hybrid Number Method. Further explanation in text.

The remaining ⅓ of the population consisting of F_1 plants would score 10 on both hybrid index and hybrid number. The resulting mean for the entire population would be 10 for hybrid index and 5 for hybrid number.

A population consisting entirely of F_1 plants, a very unlikely occurrence, would score at the apex of the triangle since this is the most hybrid a population can be. A hybrid swarm consisting of both parental species and various backcross and segregational hybrids would graph somewhere below the peak of the triangle in figure.

RESULTS

The results of scoring the population over the 22 year study period are summarized in table 4 and graphed in figure 3. Ex-

TABLE 4

The means of the hybrid index and the hybrid number of the 5 characters scored from the population sampled during the period 1958-1980.

Year	Hybrid Index	Hybrid Number
1958	8.0	5.1
1960	9.0	5.7
1962	9.6	6.7
1964	7.1	7.0
1966	8.7	8.2
1968	11.5	7.9
1970	11.0	6.6
1972	12.3	7.1
1974	13.5	7.4
1976	14.9	5.1
1978	14.3	4.3
1980	16.2	3.3

amination of the hybrid index values reveals an obvious change in the population mean from 8.0 in 1958 to 16.2 in 1980 and a change in the mean hybrid number from 5.1 to 3.3 over the same period. The population was most hybrid in 1966 and 1968 since the population was graphed for those years at points nearest the hybrid peak. The most hybrid the population would be graphed at 10.0 hybrid index and 10.0 mean hybrid number.

The population was least hybrid in 1958 and again in 1980 as indicated by the position of the glyph in 1958 (fig. 3) being located nearer the 0 end of the scales. In 1958 the population contained a greater number of *H. divaricatus,* while the 1980 sample contained a greater proportion of *H. microcephalus.* The population has become polarized toward *H. microcephalus,* particularly since 1966. The greatest change in the hybrid nature of the population occurred between 1966 and 1968 since the population

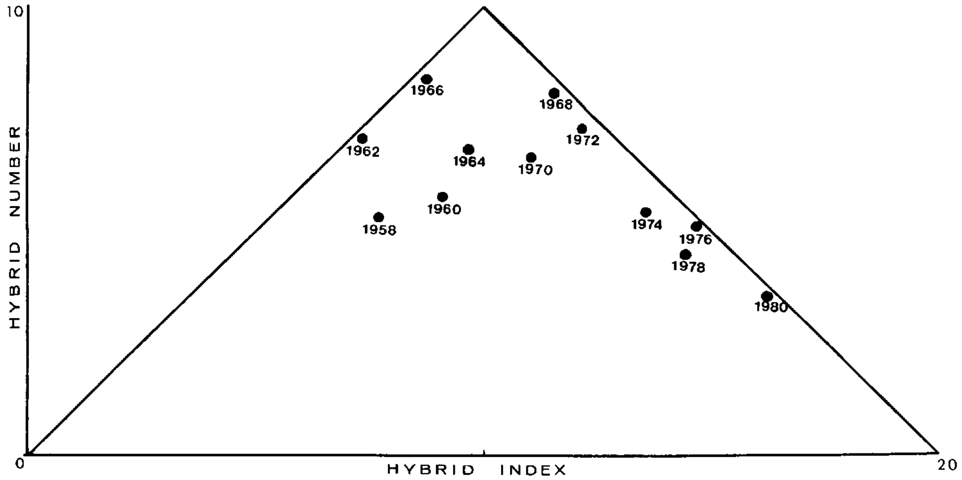

FIGURE 3. Graph of the mean hybrid number against the mean hybrid index for the population sampled from 1958-1980. Further explanation in text.

contained plants more characteristic of *H. divaricatus* in 1966 and a complete shift to more plants representative of *H. microcephalus* in 1968. Finally, by 1980 the hybrid swarm has become less hybrid and more characteristic of *H. microcephalus*. This shift appears to be correlated with the change in the habitat as a result of the abandonment of the telephone line in 1962 followed by a lag period, as would be expected.

While no precise determination of the size of the hybrid swarm was made, an estimate was conducted at five different times during the study period (table 5). Since 1962, the year the telephone line was abandoned, the population has undergone a significant decrease in size from a high of 1215 to a low of 350 plants in 1980.

TABLE 5

Population size (n) of Helianthus divaricatus x H. microcephalus hybrid swarm, 1958-1980.

yr.	1958	1962	1968	1972	1980
(n)	915	1215	938	523	35

DISCUSSION

The primary objective of this investigation was to study and record the changes in a hybrid swarm over a 22 year period of time during which there were successional changes in the habitat. In 1958, the vegetation of the study area was controlled by the annual cutting of sprouts of woody species consisting primarily of oak, maple and hickory, although occasional plants of mulberry, black cherry, ash and poison ivy were noted. A few species of herbaceous perennials also were present. The most abundant were species of *Prenanthes, Solidago, Oxalis* and *Geranium.*

In addition to the decrease in the overall size of the population, a major shift has occurred in the ratio of plants representative of the parental species to their hybrids. The population was more hybrid in nature between 1966 and 1968, therefore fewer plants representative of the parental species were present. It is significant that, since 1968, the population has changed from predominantely hybrid in nature to one consisting predominately of *H. microcephalus*-like plants. The hybrid nature of the population is decreasing as the habitat reverts to one more favorable to *H. microcephalus.*

Should the present trend continue, it is unlikely in the near future that the population will contain either *H. divaricatus* or hybrids. However, the genetic incorporation of *H. divaricatus* into the gene pool of *H. microcephalus* has occurred, at least in this local population. The next immediate question is whether or not these genes will spread to surrounding populations. Theoretically, three events may occur in the future. First, the entire population of these species and their hybrids may not survive the habitat change. In this event there will be no significant evolutionary effect of hybridization. Second, genes of *H. divaricatus* now incorporated in the *H. microcephalus* gene pool may not only continue to be fixed in the population but may spread to surrounding populations of either parental species. Since the habitat is now more favorable to *H. microcephalus, H. divaricatus* is not likely to survive. However, should *H. divaricatus* survive, the opposite could occur; that is, the surrounding populations of *H. divaricatus* could become more variable due to the introgression of genes from *H. microcephalus* or their hybrids. *Helianthus microcephalus* is the more common species in this area. It is intended that this investigation continue in an attempt to determine whether or not the surrounding populations of these species of sunflowers exhibit variation that could be attributed to introgressive hybridization.

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ANNOUNCEMENT

The American Association for Clinical Chemistry will present its "Award for Outstanding Contributions through Service to Clinical Chemistry" to one of its most conscientious and dedicated members, Dr. Samuel Meites, Director of the Clinical Chemistry Laboratory at Children's Hospital in Columbus, Ohio. Dr. Meites received an A.B. in botany and chemistry from the University of Missouri in 1942 and a Ph.D. in biochemistry from Ohio State University in 1950. A professor in the departments of Pediatrics and Pathology at the Ohio State University College of Medicine, Dr. Meites had edited 6 scientific texts, including the 1977 and 1981 editions of *Pediatric Clinical Chemistry.* Dr. Meites has been a member of the Ohio Academy of Science for over 15 years and has been nominated for fellowship.